

Vertical migrations in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae)

M. Vannini¹, R. K. Ruwa²

¹ Dipartimento di Biologia Animale e Genetica dell'Università degli Studi di Firenze, v. Romana 17, I-50125 Firenze, Italy, and Centro di Studio per la Faunistica ed Ecologia Tropicali del CNR, v. Romana 17, I-50125, Firenze, Italy

² Kenya Marine and Fisheries Research Institute, Mombasa P.O. Box 81651, Kenya

Received: 12 July 1993 / Accepted: 16 September 1993

Abstract. *Sesarma leptosoma*, somewhat similar to the Atlantic related species, *Aratus pisonii*, is an East-African mangrove crab which spends its entire life on the roots and branches of mangrove trees (mostly *Rhizophora mucronata*, *Bruguiera gymnorhiza* and *Ceriops tagal*). *S. leptosoma* never enters the water, nor does it ever venture onto the free mud surface at low tide. Part of the day and night it remains on the lower parts of the mangrove aerial roots, which are often encrusted with a wet algal mat of *Bostrichia* spp., searching for food and water. Twice a day, from ca. 06:00 to 08:00 hrs in the morning and 16:00 to 18:00 hrs in the afternoon, many of the crabs migrate as far as the leaves at the top of the tree on which they feed. However, they only spend a brief period among the leaves, from ca. 07:00 to 10:00 and 17:00 to 19:00 hrs, after which time they make their way back towards the roots again in two downward migrations. In the morning, the downward migration brings all the crabs back to the roots, but in the evening not all the crabs take part in the downwards migration and some of them pass the whole night in the tree tops. A comparison of the migration time patterns for two different periods of the year (June–July and November) shows that the number of crabs migrating along the tree trunk is modulated by the spring-neap tidal cycle, while the onset of daily migration seems to be controlled mostly by the light level and/or other climatological cues. The adaptive significance of this migratory behaviour is discussed. Observations reported in our study were made in Mida Creek, Dabaso, Kenya in 1991 and 1992.

roots and periodically venture onto the mud surface; others (C) live exclusively on tree trunks and roots which they rarely abandon; and, finally, yet others (D) inhabit the whole of the tree, invading the terminal branches and leaves, and never wander as far as the ground (Ruwa 1990, Vannini et al. 1994).

In both the Indo-Pacific and West-Atlantic mangrove areas, various decapod species can be found living in equivalent conditions. Generally, more species occur in the Indo-Pacific area, with the exception of Category D. Until now this category was only represented by *Aratus pisonii* (Hartnoll 1965, Von Hagen 1977), a tropical West Atlantic species, the only crab able to feed on mangrove leaves [recently an East Atlantic form has been proposed as a distinct species, *A. elegans* (Green 1986) quoted in Hartnoll (1988), but no references are yet available on its ecology and behaviour].

After several expeditions to the Somalian and Kenyan mangroves, from 1971 to 1988, one species (*Sesarma leptosoma*, Sesarminae) was found which can be considered ecologically equivalent to *Aratus* species. One basic difference between *S. leptosoma* and *A. pisonii* may explain why the arboreal habit of the former species has never been observed, i.e., its occurrence among the leaves is restricted to two short periods per day, one early in the morning and the other just before sunset.

The present paper aims to describe the quantitative and temporal migration patterns of a large population of *Sesarma leptosoma* found in a Kenyan locality.

Materials and methods

Sesarma leptosoma Hilgendorf, 1869 is a small, elusive crab (ca. 2 cm carapace length), previously only described for East Africa by Hartnoll (1975) in Tanzania. In Kenya it is very common in one locality in Mida Creek (Dabaso), but it has never been found (in spite of consistent research efforts) in the Shimoni, Gazi or Ngomeni mangroves, nor in any of the other localities within Mida Creek itself (Mida, Sita). After the first discovery of the species in 1988, more detailed observations were made in Mida Creek in November 1991 and June–July 1992.

Introduction

Among the many species of decapods living in mangrove swamps, a substantial group (mostly Grapsidae – Sesarminae and Grapsinae – some Xanthoidea and Anomura) is capable of climbing trees. Some species (A) are terrestrial and can occasionally climb the mangrove root system; other species (B) basically live among the

A very tall tree (*Rhizophora mucronata*) was chosen for the observations (12 to 13 m high) with a well developed root system inhabited by a large crab population which was easily visible round most of the circumference. Two reference points, 4.5 m apart, were chosen along the trunk, the lower just above the aerial roots and the higher just above the first branch bifurcation. The crabs spent most of the time among the roots or branches and only occupied the tract between the two reference point during migration.

Observations were made at a distance of 20 m through binoculars, by scanning the visible trunk surface between the two reference points. The number of migrating crabs was recorded every 5 min, noting their direction and sized (small, medium, large). When necessary an electric torch was coupled to the binoculars.

After the first 2 d of nearly continuous observations it became clear that at certain times of the day and throughout the night the crabs stopped migrating completely. Observations were carried out continuously over the following days (every 5 min) from 5:00 to 10:30 and from 15:00 to 20:00 hrs. The trunk was checked at random during the remaining periods and no migratory activity was observed.

Each record consisted of two separate observations (each lasting 40 to 80 s) taken from two observation points almost opposite each other. In this way, nearly 85% (ca. 315 degrees) of the circumference of the tree could be observed. Consequently, all the figures in the text have been increased by 15% to give a rough estimate of the number of crabs present on 100% of the trunk surface between the two reference points.

Periodically crabs from four other trees were inspected, which proved to be homogeneous with the population under observation.

The speed of some crabs as they migrated between the two reference points (ten migrating upwards and 15 downwards) was estimated using a video camera. The fastest crabs walked at 94.8 cm min⁻¹ (downwards) and 70.2 cm min⁻¹ (upwards) but the average speed was 25.2 and 51.0 cm min⁻¹ downwards and upwards, respectively. The fastest crab recorded took approximately 5 min to run between the two reference points (4 min 42 s, upwards, and 6 min 24 s, downwards). Recording the number of crabs every 5 min guarantees that all the crabs are counted, but not that the crabs are different at each observation.

Sources of error

(a) In dim light, the smaller specimens were not easily detectable, resulting in an underestimate of the number of individuals at certain hours of the day, especially when it was very cloudy.

(b) The section of the trunk which could not be observed was always overshadowed by other thick trees. During the sunny hours, the crabs preferred the part of the trunk in the shade. The true number of crabs congregating along the hidden strip is unknown and in certain cases could be quite different from the results of the extrapolation obtained (see previous paragraph). The final effect should be a certain underestimate for the sunnier hours, especially on the sunniest days.

(c) Strong winds tend to slow down crab speed. Crab speed is probably also affected by temperature and other climatic factors. The effect is an unpredictable overestimate in the number of crabs (if slow) or underestimate (if fast).

Tides

The tidal pattern in the creek reflects the oceanic variation (two tides a day) with an average (six measurements) delay of 1 h 08 min (95% confidence limits: 1 h 02 min to 1 h 13 min) with respect to the Kilindini tide tables. At ST (Spring Tide) the mud surface, where observations were concentrated, began to flood ca. 2 h before the creek HW (High Water).

At EHWST (Extreme High Water Spring Tide), the creek HW level is ca. 0.4 m lower than the open ocean level. The tree roots in the study area were always flooded twice a day. At the lowest HWNT (High Water Neap Tide) the water just reached the roots, whilst at EHWST they were covered by 120 to 170 cm of water.

Results

Zonation

The crabs were seen on the roots and trunks of *Rhizophora mucronata*, *Cerriops tagal* and *Bruguiera gymnorhiza*. On the contrary, *Avicennia marina* and *Sonneratia alba* were rarely inhabited, probably because their distribution (mostly landwards in the case of the former and seawards in the latter) does not correspond to the crabs' preferred zonation (roughly the central part of the mangrove belt; Vannini et al. 1994). Crabs may proceed as far as the base of the roots, where they feed on the mud but they never venture onto the mud itself.

The crabs were rarely seen on small trees and seem to prefer taller ones (a 12 to 15 m high *Rhizophora mucronata* can host several hundred individuals). This preference can, at least in part, explain the odd distribution of this species. Dabaso is the only Kenyan locality (at least of those visited) where a few acres of tall *R. mucronata* still survive intact and are almost undamaged from the heavy felling activity so widespread along the Kenyan coast.

Migration

The crabs can only be seen on the trunk at certain times of the day, during their active migrations from roots to branches and leaves or vice versa.

Vertical migration occurs twice daily: from approximately 06:00 to 10:00 and 16:00 to 19:00 hrs. Both migrations consist of an upwards and a downwards flow, resulting in four different flows: morning up (MU), morning down (MD), evening up (EU) and evening down (ED).

Number of migrating crabs

The number of crabs migrating varies from day to day. Averages are given in Table 1.

More crabs were seen in 1992 than in 1991. The upwards and downwards flows appear to be similar only in the morning 1992. Since the two flows must obviously always be equal, we can presume that the observed discrepancies must be due to some of the error sources mentioned above.

In both years, more crabs participated in the MD than MU migrations (in 1992 the two flows appear equal, but the MD flow is probably underestimated) while the opposite is true in the evening as EU is larger than ED.

Daily variation is very high and not all the above differences proved to be significantly different (the only significant differences, at least at a level of 0.05, after applying the *t*-test were EU₉₁ vs ED₉₁, EU₉₂ vs ED₉₂, MU₉₁ vs MD₉₁, MU₉₁ vs MU₉₂).

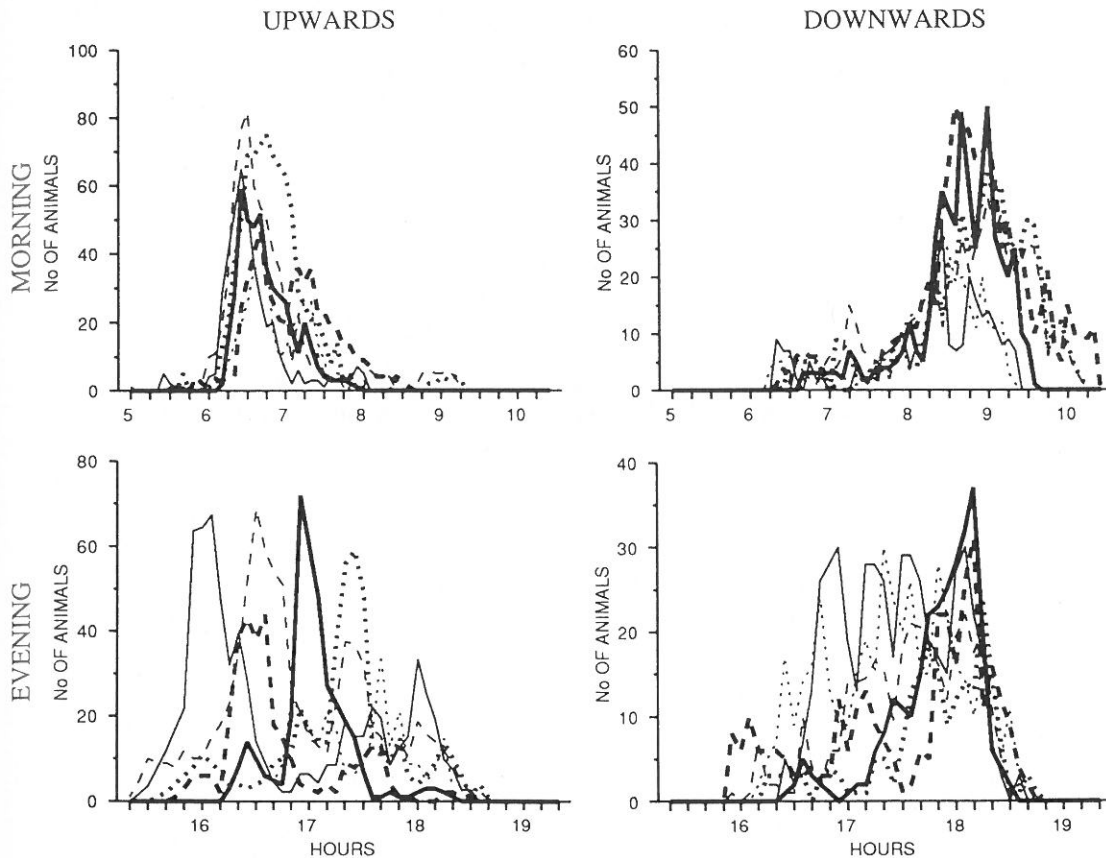


Fig. 1. *Sesarma leptosoma*. Migration flows recorded, at 5 min intervals, in November 1991. The six most intense flows out of the nine recorded are represented

Several direct inspections with a binocular confirmed that usually no crabs could be seen among the leaves and branches during the day, at least after 08:30 or before 16:30 hrs. At night, however, a few more or less immobile individuals were found among the leaves of some of the smaller trees which could be climbed by the observer.

Migration times

Detailed patterns of six migration flows for November 1991 are shown in Fig. 1. In spite of a certain variability, it is clear that practically no crabs migrate at night, i.e., before 05:45 or after 18:45 hrs, nor between 09:00 and 15:15 hrs during the sunniest hours of the day.

Averages for the 1991 and 1992 recorded migrations (Fig. 2) reveal very similar patterns, in spite of a certain variation in the absolute quantity.

By cumulating the flows for 1991 and 1992 (Fig. 3), it can be seen that the four migratory flows are concentrated within two temporal "windows", with a longer time interval between the two morning flows than between the evening ones.

From a comparison of the equivalent 1991 and 1992 flows, it is also evident that migratory activity in 1991 started earlier and ended later than in 1992. To compare activity onset and offset of the average flow patterns in Fig. 2, the same data are represented in cumulative, relative frequency (Fig. 4).

Table 1. *Sesarma leptosoma*. Average number of crabs (nc) participating in the four migrations. (n): number of recorded migrations; SE: standard error

	Morning		Evening	
	Up	Down	Up	Down
1991				
nc	333	428	300	169
n	10	10	10	10
SE	26.9	31.9	73.5	34.1
1992				
nc	522	517	400	252
n	7	6	9	9
SE	69.9	74.3	75.1	53.7

From Fig. 4 it is possible to interpolate the moment at which 50% of the crabs participating in each migrational flow was recorded (F_{50}). If this is repeated for each single migratory flow for both years, the timing of the different flows can be statistically compared (Table 2).

The variability between the two evening flows for both years is high, the difference small and not significant. Between the two morning flows variability is lower, and the difference is significant: 20 min between the two UM and 59 min between the two DM flows.

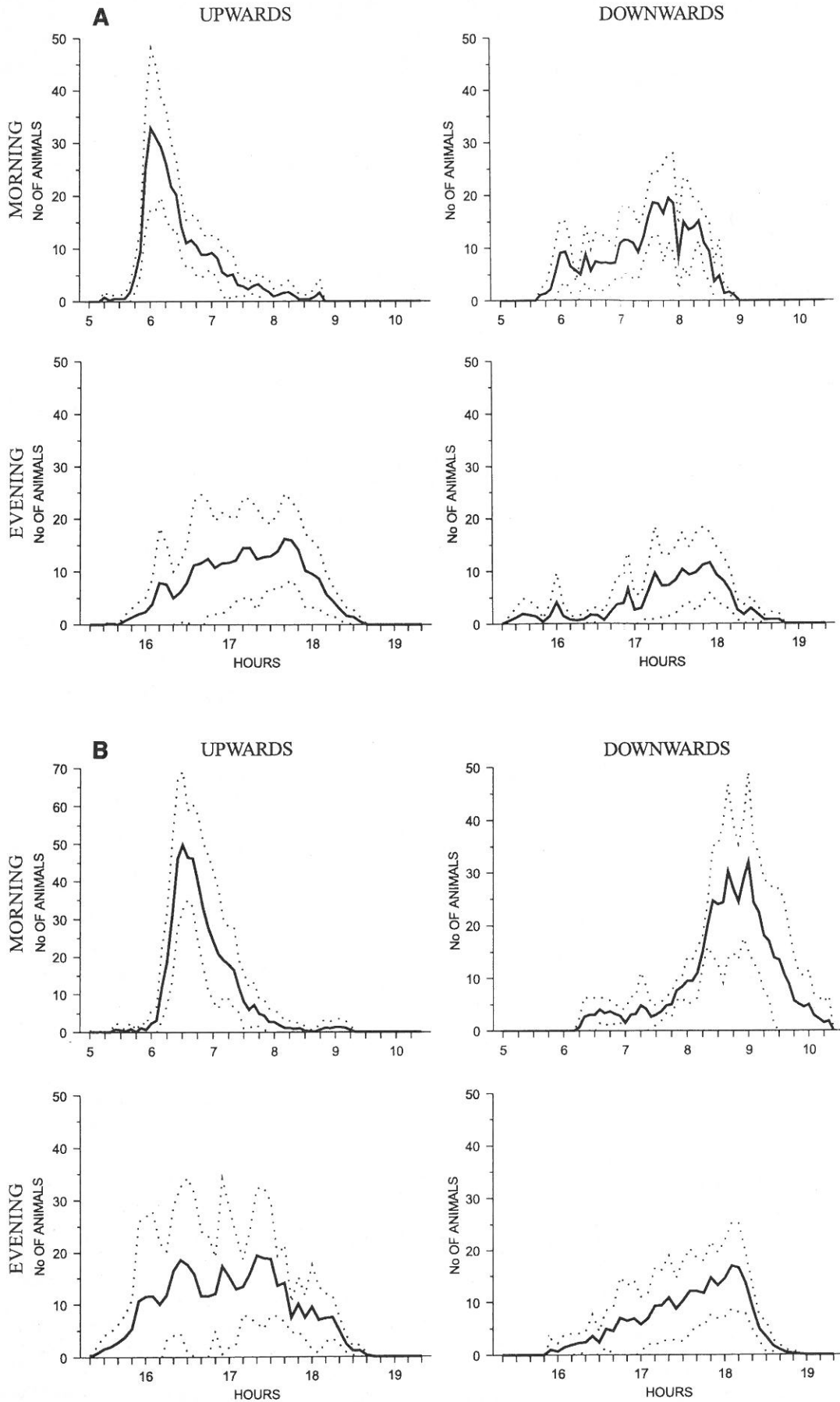


Fig. 2. *Sesarma leptosoma*. Average pattern of the four migration flows for (A) 1991 and (B) 1992. Dotted line: confidence limits (95%)

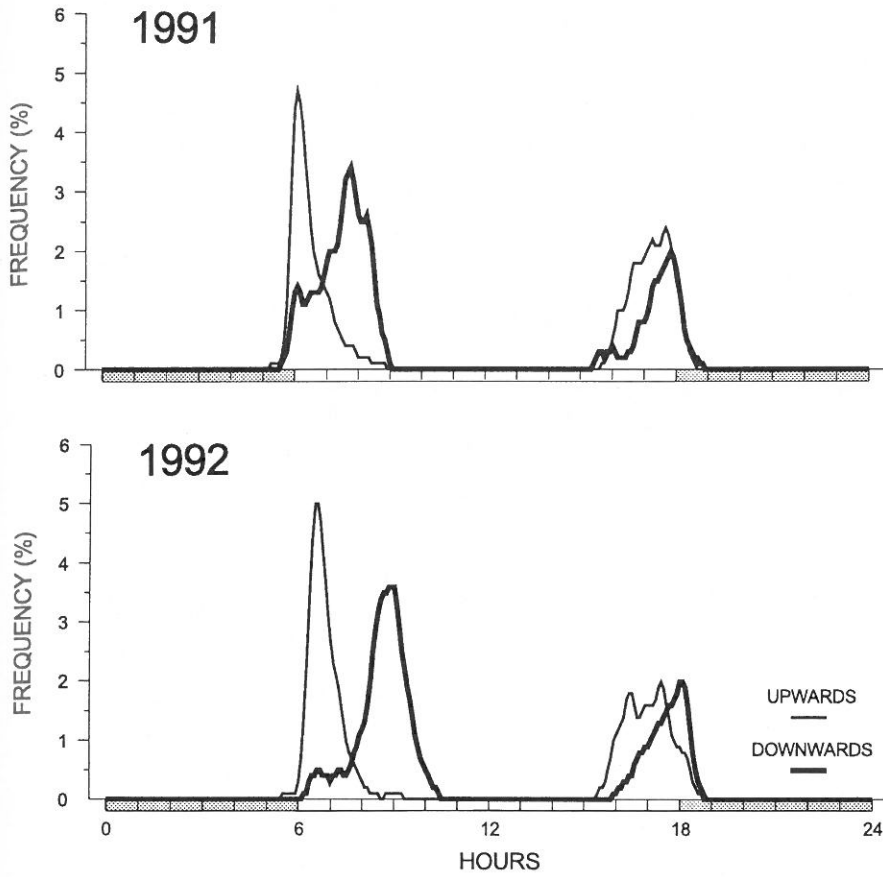


Fig. 3. *Sesarma leptosoma*. Average pattern of the four migration flows, for 1991 and 1992. Relative frequency, average number of crabs recorded each observation over the total number of crabs for each flow

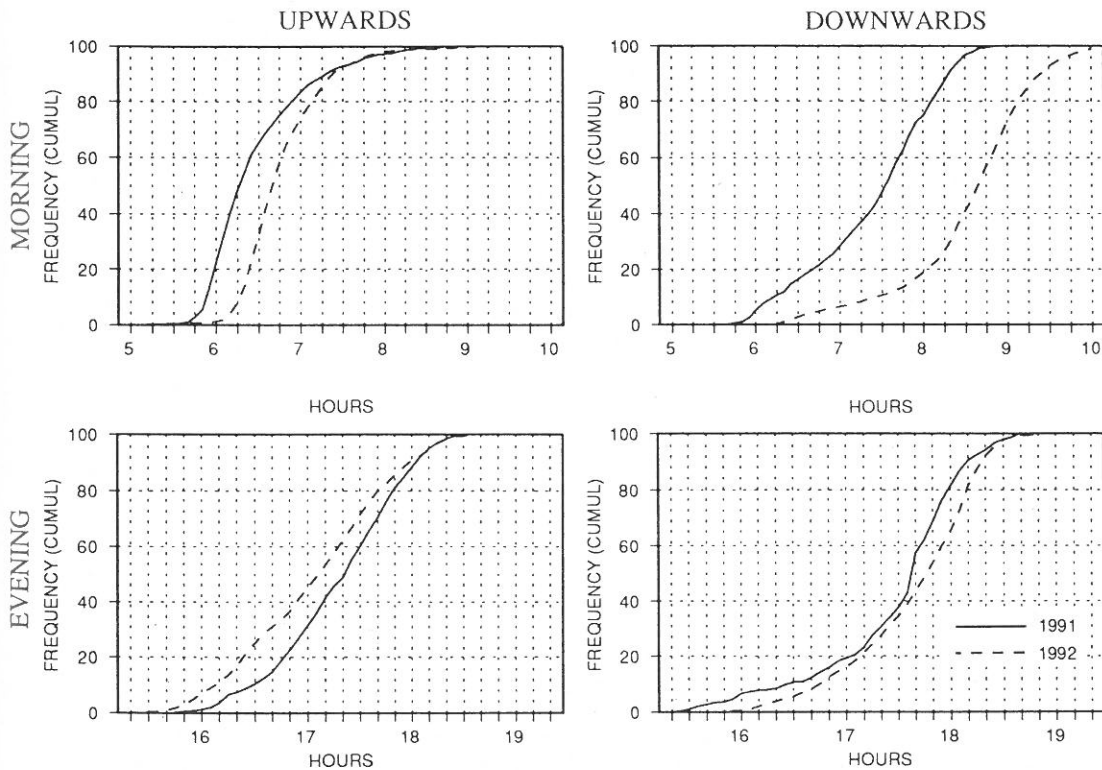


Fig. 4. *Sesarma leptosoma*. Cumulative relative frequency of migration activity in 1991 and 1992

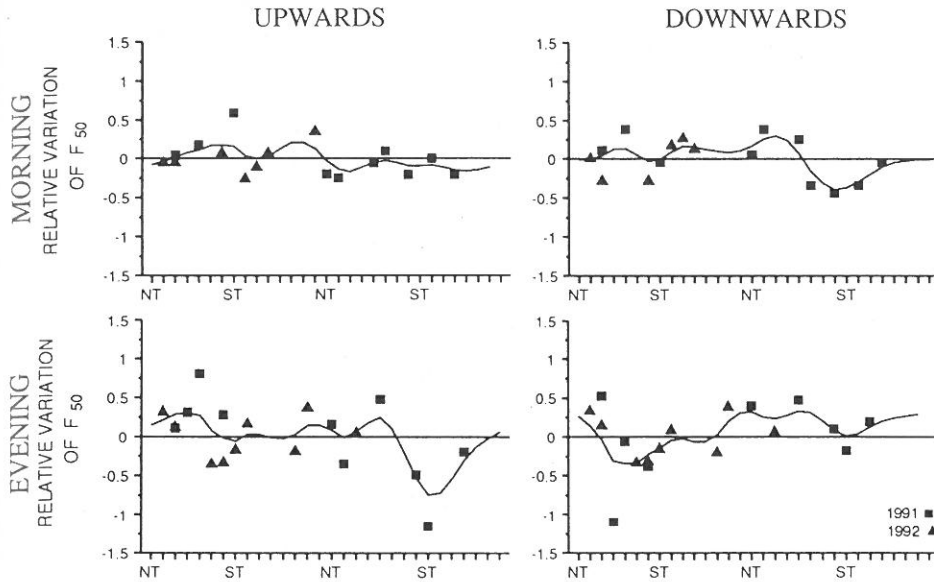


Fig. 6. *Sesarma leptosoma*. Variation in F_{50} (relative to the average F_{50} for both years) in crab migration time (F_{50}) over a synodic month. Data for 1991 and 1992 combined to allow overlapping equivalent tidal phases. NT: Neap Tide; ST: Spring Tide

Discussion

Sesarma leptosoma is a mangrove crab inhabiting the mangrove trees root system, where, like many other mangrove crabs, it can be observed wandering, grazing or hiding under bark, but also venturing onto the trunk, branches and leaves of the mangrove tree.

Until now, among the so-called "mangrove crabs", only the Atlantic species, *Aratus pisonii* (which also belongs to the sub-family Sesarminae), was known to extend its range as far as the mangrove leaves, but the life-history of *Sesarma leptosoma* seems even more tree-dependent than its Atlantic relative.

Whilst in *Aratus pisonii* the juveniles seem to inhabit the soil (Warner 1970), in *Sesarma leptosoma* all stages can be found on the tree and on the tree only. Periodic spawning migrations of females have been described in *A. pisonii* (Warner 1967); although actual spawning of *S. leptosoma* has not been observed, in June–July and October–November females with eggs were commonly seen on the trunks and roots. On no occasion or during any tidal phase were they ever observed on the mud surface.

The two species are similar in size, an adult *Aratus pisonii* measuring ca. 20.0 × 25.0 (carapace length × width) and *Sesarma leptosoma* ca. 21.0 × 25.0 mm. In 1992, over 500 *S. leptosoma* were counted in the morning, migrating along a *Rhizophora mucronata* trunk. This figure is probably an overestimate of the true number of crabs living on the tree (see "Materials and methods"). Actual population size may not have exceeded 300 crabs, more than half of which were sexually mature. This figure is quite different from the density of five to six adults per tree as recorded by Warner (1970) in *A. pisonii*.

Sesarma leptosoma is a strictly iso-phasic animal (Vannini and Chelazzi 1985), more so than *Aratus pisonii*. The former species can often be seen at the water's edge, pick-

ing up things from the surface, but it almost never goes under water, unless disturbed, while *A. pisonii* is said to continually enter and leave the water (Hartoll 1965).

Sesarma leptosoma does not reside permanently on the mangrove roots or leaves; regularly, twice a day, it shifts from the roots to the branches and vice versa, within two very narrow temporal windows. The upwards migratory flow starts at sunrise (around 06:00 hrs), followed by a downwards flow which ends before 10:00 hrs. A second upwards flow takes place between 15:00 and 16:00 hrs followed once more by a second downward flow ending around 19:00 hrs.

At night, a fraction of the crabs remains among the leaves (the downward evening flow is usually less intense than the preceding upward one), but with the following morning downward migratory flow, all the crabs make their way to the roots for the day. Practically no crabs at all occur on the trunks outside these two migratory phases.

Migrations never involve the whole crab population, only a part, and the proportion varies from day to day. The two evening migration flows, at least, seem to be modulated by the tidal phase since they diminish at NT.

A relationship exists between both the onset of the morning upwards flow and end of the evening downwards flow and sunrise and sunset times, respectively. The times of the two other migratory flows is more variable and probably depends on climatic factors. No evidence of relationship between onset time and tidal phase could be found in any of the migratory flows.

In other words, the temporal migration pattern of these intertidal crabs, subject to a change of ca. 1.5 m in water level twice a day, seems to be governed only by the light level (the crabs only actively migrate during the day) and perhaps by other factors (internal and/or external) apparently not linked to the variation in the tidal level.

In contrast, the migrations of *Aratus pisonii* do seem to depend on water level and tidal variation. Migration along the trunk is never suspended, although it is particularly intense at high tide while at low tide most individuals stay on the ground (Von Hagen 1977).

Why does *Sesarma leptosoma* migrate towards the leaves?

Eating green leaves instead of searching for yellow ones on the mud surface may increase the quality of the crabs diet and/or reduce competition for food, but no direct data are yet available to discuss these points. Staying less on the mud and on the lower tree levels will in any case reduce predation risks. The mud platform is in fact patrolled by legions of *Metopograpsus thukuhar* and *M. oceanicus* (Grapsinae), *Thalamita crenata* (Portunidae), *Eurycarcinus natalensis* (Pilumnidae), *Sesarma guttatum* (Sesarminae), and *Epixanthus dentatus* (Menippidae). Many of these crabs can occasionally climb the mangrove roots and have actually been seen preying upon *S. leptosoma* (Vannini et al. 1994). On the other hand, no potential predators were observed among the tree tops.

A rise in temperature and the need to replenish their water supply can explain why the crabs have to abandon the tree tops from ca. 10:00 to 16:00 hrs, but neither dehydration nor any of the above factors can explain why the migratory flows only take place when the light reaches a certain threshold, or why they are totally inhibited at night.

Preliminary records show that a single return trip up a 12 to 15 m high tree could take ca. 40 min if the crabs walked the whole distance at the maximum recorded speed, but more often it would probably take an average of ca. 1 1/2 h. No matter what the reasons are for climbing the trees, they must be extremely important if such a time-wasting journey (and presumably energy-wasting too) has to be taken twice a day just to stay among the

M. Vannini and R. K. Ruwa: Vertical migrations in a tree crab

thinner branches and leaves for 1.5 to 2 h in the morning and for ca. 1 h in the evening.

More knowledge on the biological and feeding biology of *Sesarma leptosoma* is needed to better discuss the adaptive value of vertical migration in crabs, as well as more details on the activity rhythm of the main mangrove predators.

Acknowledgements. Many thanks are due to Mr. R. Innocenti, Ms T. Kazungu and Ms F. Vannini for their help during field work. The work was supported by Accademia dei Lincei, a CNR grant and an EEC (STD-2) project. The mangrove crab programme would never have taken off without the help and the encouragement of our friend Prof. P. Polk (Free University of Brussels).

References

- Green, J. L. (1986). The biology of *Aratus elegans*. M. Sc. thesis, University College of North Wales
- Hartnoll, R. G. (1965). Notes on the marine grapsid crabs of Jamaica. Proc. Linn. Soc. Lond. 176(2): 133-147
- Hartnoll, R. G. (1975). Grapsidae and Ocypodidae (Decapoda: Brachyura) of Tanzania. J. Zool. Lond. 177: 305-328
- Hartnoll, R. G. (1988). Evolution, systematics and geographical distribution. In: Burggren, W. W., McMahon, B. R. (eds.) Biology of land crabs, Vol. 2. Cambridge University Press, Cambridge, p. 6-54
- Ruwa, R. K. (1990). The effect of habitat complexities created by mangroves on macrofaunal composition in brackish water intertidal zones at the Kenyan coast. Disc. Innovation 28(1): 49-55
- Vannini, M., Chelazzi, G. (1985) Adattamenti comportamentali alla vita intertidale tropicale. Oebalia (Taranto, Italy) 11: 23-37
- Vannini, M., Ruwa, R. K., Olvoch, A. (1994). The tree-climbing crabs of Kenya (Crustacea Decapoda). Trop. Zool. (in press)
- Von Hagen, H.-O. (1977). The tree climbing crabs of Trinidad. Stud. Fauna Curaçao 54: 25-59
- Warner, G. F. (1967). The life history of the mangrove tree crab *Aratus pisoni*. J. Zool. Lond. 153: 321-335
- Warner, G. F. (1970). Behaviour of two species of grapsid crabs during intraspecific encounters. Behaviour 36: 9-19

Communicated by M. Sarà, Genova